Journal of Physiology (1989), **413**, *pp.* 107–118
With 6 text-figures
Printed in Great Britain

SPATIAL SPREAD OF IN-FIELD AFFERENT INHIBITION IN THE CAT'S SPINOCERVICAL TRACT

BY R. NOBLE* AND A. D. SHORT

From the Department of Preclinical Veterinary Sciences, University of Edinburgh, Summerhall, Edinburgh EH9 1QH

(*Received 6 December 1988*)

SUMMARY

1. Extracellular microelectrode recordings were made from twenty-three spinocervical tract (SCT) cells in the lumbar spinal cord of cats anaesthetized with chloralose and paralysed with gallamine triethiodide. Excitation and inhibition of the cells were elicited by applying small brief (4 mN, 60 ms) localized jets of air to the clipped hair in and around the receptive fields.

2. Receptive field extents ranged from 40 to 180 mm. Excitation occurred in the period 30–130 ms after the start of the stimulus, and in-field afferent inhibition from 130 ms up to 700 ms or more. The inhibition was manifest as a reduction in background discharge and as a reduction in responsiveness to a test stimulus which followed a conditioning stimulus.

3. When the conditioning stimulus was spatially separated from the test stimulus, the degrees of in-field afferent inhibition depended on the spatial separation, even when both were within the excitatory receptive field. The spatial spread of in-field afferent inhibition was limited to 100 mm or less.

4. In two units only, afferent inhibition was produced from a narrow strip just outside the excitatory receptive field. In the other units, it could only be produced from within the excitatory receptive field.

5. The results suggest that the inhibitory input to SCT cells is organized in subdomains no more than 100 mm across, which may correspond to the receptive fields of interneurones between the primary afferent fibres and the SCT cells.

INTRODUCTION

Spinocervical tract (SCT) cells in the cat receive both mono- and polysynaptic excitatory input from group II hair follicle afferent fibres. In the majority of cases this connection is very efficient, with more than a 50% probability that a single afferent impulse will elicit one or more impulses in a SCT cell (Brown, Koerber & Noble, 1987*a*). Following excitation, however, by a single action potential in a hair follicle afferent fibre, there is a period lasting 700 ms or more when the response to

* Present address: Department of Physiology and Biochemistry, University of Reading, Whiteknights, Reading RG6 2AJ.

a second excitation is reduced; the movement of a discrete group of hairs in the excitatory receptive field will also produce a long-lasting reduction in responsiveness (Brown, Koerber & Noble, 1987*b*). The reduction is not associated with any inhibitory postsynaptic potentials (IPSPs) in the SCT cells (Brown, Koerber & Noble, 1987*c*) and recurrent inhibitory effects and post-activation depression of the SCT cells have been ruled out. We have adopted the term 'in-field afferent inhibition' (Laskin & Spencer, 1979) for this phenomenon. We do not know its mechanism or site, except that it must occur presynaptically to the SCT cells, possibly on interneurones mediating the polysynaptic input or on the synapses of the afferent fibres (Hongo, Jankowska & Lundberg, 1968; Brown *et al.* 1987*c*). The in-field afferent inhibition lasts longer than, and is quite distinct from, the inhibition of SCT cells producing IPSPs with a latency of 20–40 ms. This latter inhibition results from a stimulus to inhibitory receptive fields different from, but often overlapping, the excitatory receptive fields of SCT cells and is thought to be mediated by group III hair follicle afferent fibres and other low-threshold mechanoreceptor afferents from glabrous skin (Brown *et al.* 1987*c*).

The in-field afferent inhibition of transmission between hair follicle afferent input and a SCT cell can be evoked from throughout the excitatory receptive field (Brown *et al.* 1987*b*, *c*). Similar afferent inhibition has been reported in cat cuneothalamic cells (Jänig, Schoultz & Spencer, 1977), cat thalamocortical cells (Jänig, Spencer & Younkin, 1979), cat (Laskin & Spencer, 1979) and monkey (Gardner & Costanzo, 1980) cortical cells. The present study arose from the following questions about the spatial spread of in-field afferent inhibition of SCT cells. (1) Is the response to a stimulus to one point in the excitatory receptive field suppressed by a similar preceding stimulus to another point in the field? (2) If so, what is the spatial extent of this inhibition? Can the afferent inhibition be elicited from outside the excitatory receptive field? (3) Finally, are there any directional features to in-field afferent inhibition? Is it the case that although a stimulus at one location influences the response at another location this occurs to a lesser degree, or not at all, when the stimuli are given in the reverse order?

A preliminary report of some of this work has been published (Noble & Short, 1988).

METHODS

Experiments were performed on nine young adult cats (2·35–4·5 kg body weight) anaesthetized with α-chloralose (70 mg kg^{-1}), after induction of anaesthesia with 4% halothane in a $N_2O:O_2$ mixture, and paralysed with gallamine triethiodide. Carotid arterial blood pressure, end-tidal CO_2 and rectal temperature were continuously monitored and kept within normal limits. End-tidal CO_2 was kept between 3·5 and 4·0% by adjusting the rate and stroke volume of the respiratory pump. Rectal temperature was maintained at 38–39 °C with a thermostatically controlled electric heating blanket under the animal. The level of anaesthesia was checked throughout the experiment by examination of the arterial pressure record and the degree of pupillary constriction. Additional doses (100 mg) of α-chloralose were given if the arterial pressure increased and the pupils started to dilate. Laminectomies were performed, exposing the spinal cord in the cervical region from segements C1 to C4 inclusive and in the lumbosacral cord from around L4 to S3. The animals were firmly fixed in a spinal frame and bilaterial pneumothoraces were performed to improve cord stability. Two pairs of bipolar Ag–AgCl ball electrodes were placed on the surface of the dorsolateral fasciculus at the level of the C3 root entrance zone and just rostral to the C1 root

entrance zone respectively to allow stimulation of the dorsolateral tract and antidromic identification of SCT cells. The dorsal columns were sectioned at C4 to prevent activation of dorsal column axons.

Glass capillary microelectrodes filled with 4 M-NaCl (10–20 MΩ) were used to record extracellularly from SCT cells in the lumbosacral dorsal horn. Cells were identified electrophysiologically as belonging to the SCT by their antidromic excitation from the ipsilateral dorsolateral funiculus at C3 and by the lack of such activation from C1. The receptive fields of these cells were delineated and characterized with hand-held brushes and probes, and were tested for mechanical nociceptive input with toothed clips.

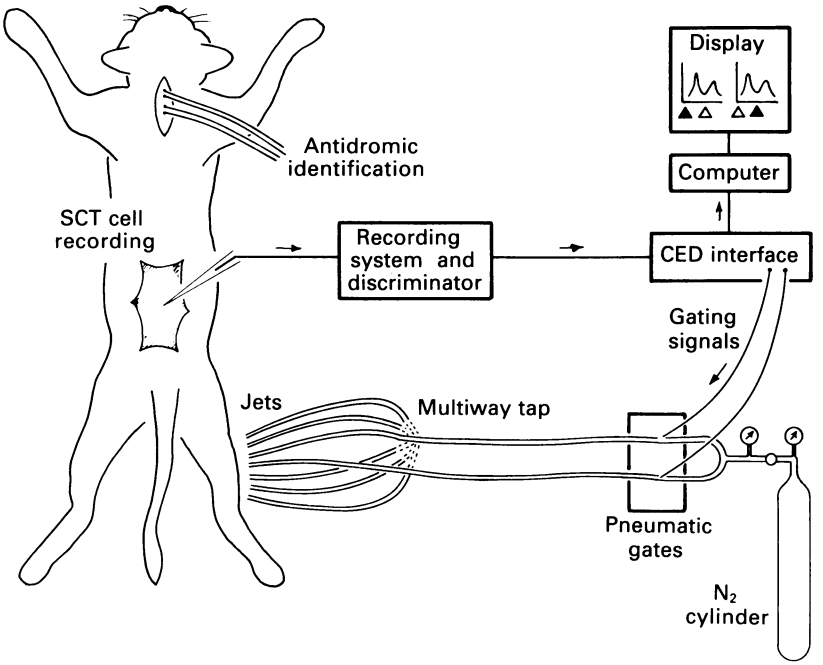

Fig. 1. Diagram of the experimental arrangement. See text for details.

The experimental arrangement is shown in Fig. 1. An array of up to nine nozzles (21-gauge hypodermic needles with the bevels removed) was positioned across the receptive field, approximately 3 mm from the surface. Each stimulus was a 60 ms gated jet of nitrogen of 4 mN force. Two of the nozzles were selected for a fixed sequence of stimulus presentations which was repeated 50 or 100 times. Stimulus presentation and timing, together with data collection, were controlled by a programmed laboratory interface and computer (CED 1401, Cambridge Electronic Design, UK, hosted by a BBC B microcomputer, Acorn, UK). The intervals between stimulus presentations was 1·5 s, and the stimuli presented were rotated in a fixed sequence. In early experiments a fourfold rotation was adopted: stimulus *a* alone, stimulus *b* alone, stimulus *a* followed by *b*, stimulus *b* followed by *a*. When both stimuli were presented the separation was between 100 and 300 ms. The fourfold rotation showed that the unconditioned responses were constant, whether or not they were followed by the other stimulus; this implied that there were no residual effects from the different presentations 1·5 s earlier. In later experiments the single stimulus presentations were not used and the double presentations were alternated: stimulus *a* followed by *b*, stimulus *b* followed by *a*.

Action potentials were converted into standard pulses which were detected by the interface and accumulated by the programme into separate peristimulus time histograms for each stimulus presentation. The histograms were displayed on the computer screen as they accumulated, and when complete were stored on disc. For each unit a 'counting time-window' was selected by

inspection of a trial histogram to include the period of the response. The 'time-window' was continuously displayed with the histograms so that it could be seen if its limits needed adjusting. In all cases the time-window was 100 ms in duration, and usually its limits were 30 and 130 ms after the initiation of the stimulus; in some cases the time-window was up to 10 ms earlier or later. The programme recorded the number of action potentials in the time-window after each stimulus: at the end of the required number of sweeps the average response (number of action potentials in the time-window) was calculated for each stimulus and a statistical test of significance (Student's t test) was made between unconditioned and conditioned responses. Background activity was counted in the interval of each sweep before the first stimulus and was scaled to correspond with the duration of the counting time-window (number of impulses in 100 ms).

One of the nozzles (usually the central one) was activated during a series of trials in which it was tested against each of the others in turn, selected by a multiway tap. For each series of trials across a receptive field, the average responses and standard errors of the unconditioned responses and of the background activity were plotted on a composite graph against distance on the skin from the fixed stimulus; the conditioned responses were displayed as percentages of the unconditioned responses with statistically significant differences ($P < 0{\cdot}05$) highlighted. These graphs (Figs 3, 4 and 5*A*) were plotted by the program as the experiment progressed. Individual histograms (Figs 2 and 5*B* and *C*) were plotted later after recalling the data from disc.

RESULTS

Twenty-three SCT units with conduction velocities between 32 and 70 m s^{-1} were studied. Excitatory receptive fields were predominantly in the lateral half of the left hindlimb, with examples from the base of the tail to the foot pads. Two of the units responded to hair movement only, the others to both hair movement and noxious pressure. The larger receptive field sizes (up to 180 mm maximum diameter) were in the proximal limb and the smaller (down to 40 mm maximum diameter) were on the foot. Searches for units were concentrated on finding the large fields; the sample is therefore biased in favour of units with larger, more proximal receptive fields.

TABLE 1. The effect of a conditioning stimulus on the background discharge of six SCT units in the period 130–230 ms after the initiation of the conditioning stimulus. The significance of the changes was calculated by Student's t test

Background (impulses/s, mean ± S.E.M.)	100–130 ms (mean ± S.E.M.)	Change	%	n	P
3·8 ± 0·49	2·3 ± 0·49	−1·5	−39	5	< 0·01
6·6 ± 0·52	2·6 ± 0·30	−4·0	−60	6	< 0·01
2·8 ± 0·17	1·7 ± 0·49	−1·1	−39	4	0·06
5·7 ± 1·26	1·5 ± 0·29	−4·2	−73	8	< 0·01
3·3 ± 0·56	0·7 ± 0·12	−2·6	−79	10	< 0·01
3·3 ± 0·56	0·6 ± 0·23	−2·7	−81	9	< 0·01

Effect of conditioning stimulus on background discharge

In seven units, where the fourfold rotation was used (including histograms where the stimuli were given singly) it was possible to measure the effect of a conditioning stimulus on the background discharge, after the initial excitation. Table 1 shows the background discharges and the mean impulse count in the period 130–230 ms after the initiation of the stimulus, a period which immediately followed the excitatory response. In all units there is suppression of the background, the reduction ranging

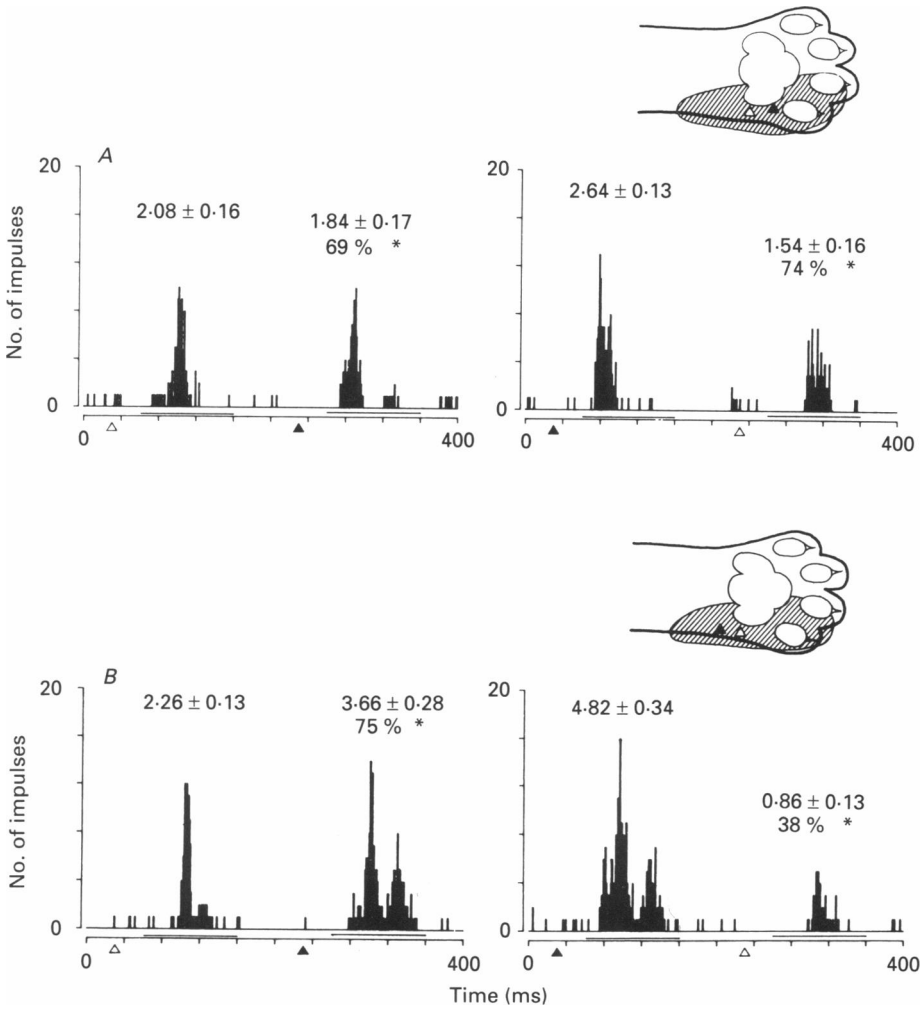

Fig. 2. Receptive field and peristimulus time histograms of the responses of a hair-and-pressure SCT cell to conditioning and testing by localized puffs of N_2 (4 mN, 60 ms) within the receptive field. Triangles indicate the location within the receptive field and the time of onset of each stimulus: △ shows that the corresponding stimulus was identical in *A* and *B*; ▲ shows stimuli at different locations in *A* and *B*. Stimulus separations were 9 mm in *A*, 8 mm in *B*. The labels show mean responses and standard errors and conditioned responses as percentage of unconditioned responses. Asterisks indicate significant inhibition ($P < 0{\cdot}05$, Student's *t* test). Binwidth 1 ms, 50 sweeps.

from 39 to 81 % and being statistically significant in all but one unit (Student's *t* test).

Effect of conditioning on a test within the excitatory receptive field

Figure 2*A* shows a peristimulus time histogram from a typical trial where the jets were 9 mm apart near the middle of a receptive field of about 50 mm in length. Each response suppressed the other to about 70 % of control value. Fig. 2 shows another

trial where one stimulus (△) is at the same position as in the previous example and the other is 8 mm away, on the opposite side and in a more sensitive part of the receptive field. The stimulus producing the bigger response produces a much greater proportional inhibition of the other than *vice versa*. This typical finding is apparent

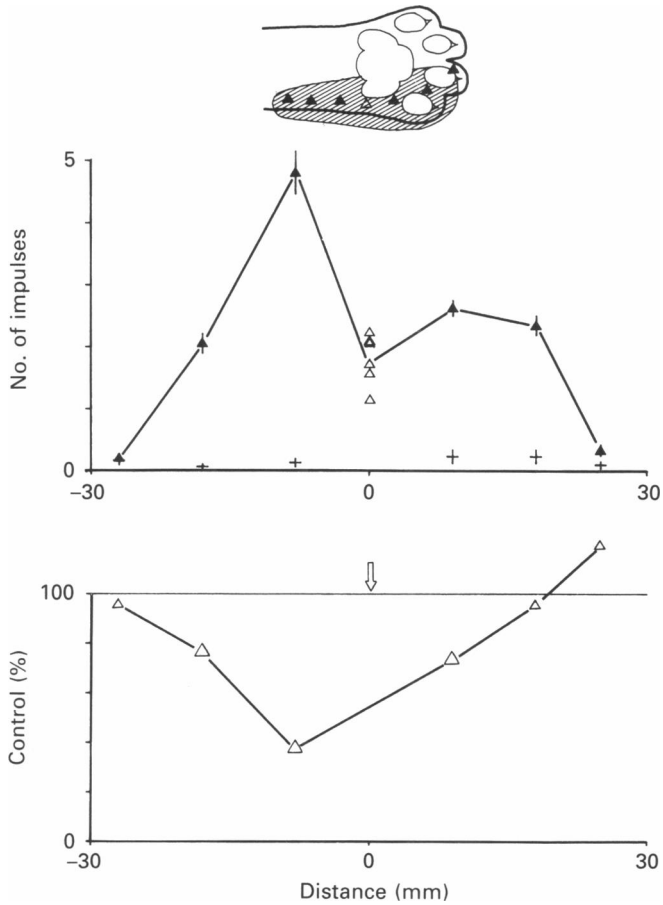

Fig. 3. Summary of six conditioning–testing trials on the unit of Fig. 2, including the two trials shown in Fig. 2*A* and *B*. Upper diagram: △, the six mean unconditioned responses to a stimulus to the fixed point; ▲, the mean unconditioned responses and standard errors (bars) at the points indicated, plotted against distance from the fixed point; +, mean and standard error of the background discharge during the six trials. Lower diagram: the responses at the fixed point when conditioned 200 ms earlier by a stimulus to the six other points, expressed as a percentage of the unconditioned response, and plotted against the distance of the *conditioning* stimulus from the fixed point (arrow on abscissa). The larger triangles indicate significant inhibition ($P < 0{\cdot}05$, Student's t test). In this unit, with a receptive field about 50 mm long, the spread of inhibition almost corresponds to the excitatory receptive field.

in the same composite diagram (Fig. 3) which includes the two examples shown in Fig. 2. In the upper half of the Fig. 3 the filled triangles show the average responses (with standard errors) to the air jets at different positions in the receptive field. The open triangles show the average responses at the fixed point while each of the other positions was tested. These therefore act as a test of the stability of the preparation,

and in this case show the common finding of a decline in response to repeated stimulation of the same position. The crosses show the averages and standard errors of the background activity at the time of each trial.

In the lower half of Fig. 3 the open triangles show the inhibitory effect of the variable position jets on the response to the fixed jet. The in-field afferent inhibition

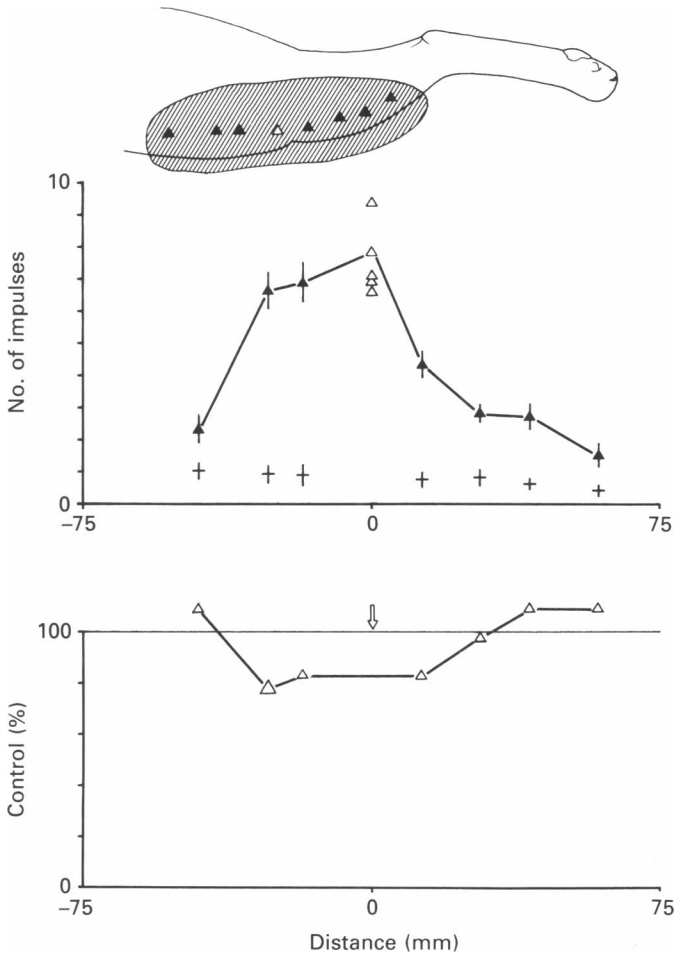

Fig. 4. Summary of responses of a hair-and-pressure SCT unit to hair movement. The symbols are described in the legend to Fig. 3. This receptive field is about 140 mm long. The upper diagram shows that it extends beyond the outermost points tested in these trials. The lower diagram shows that the spatial spread of in-field afferent inhibition is restricted to a subdomain about 60 mm long.

declines with distance in a manner which parallels the excitatory receptive field with one exception (where there is excitation but no inhibition of the other response). Not shown in Fig. 3 is the inhibition in the opposite direction, of the variably positioned stimuli by the fixed stimulus. This has been omitted for clarity; its characteristics are similar to the inhibition shown when both responses are of similar magnitude, but towards the edge of the excitatory receptive field responses are small and of comparable magnitude to the background discharge; the observed inhibition is

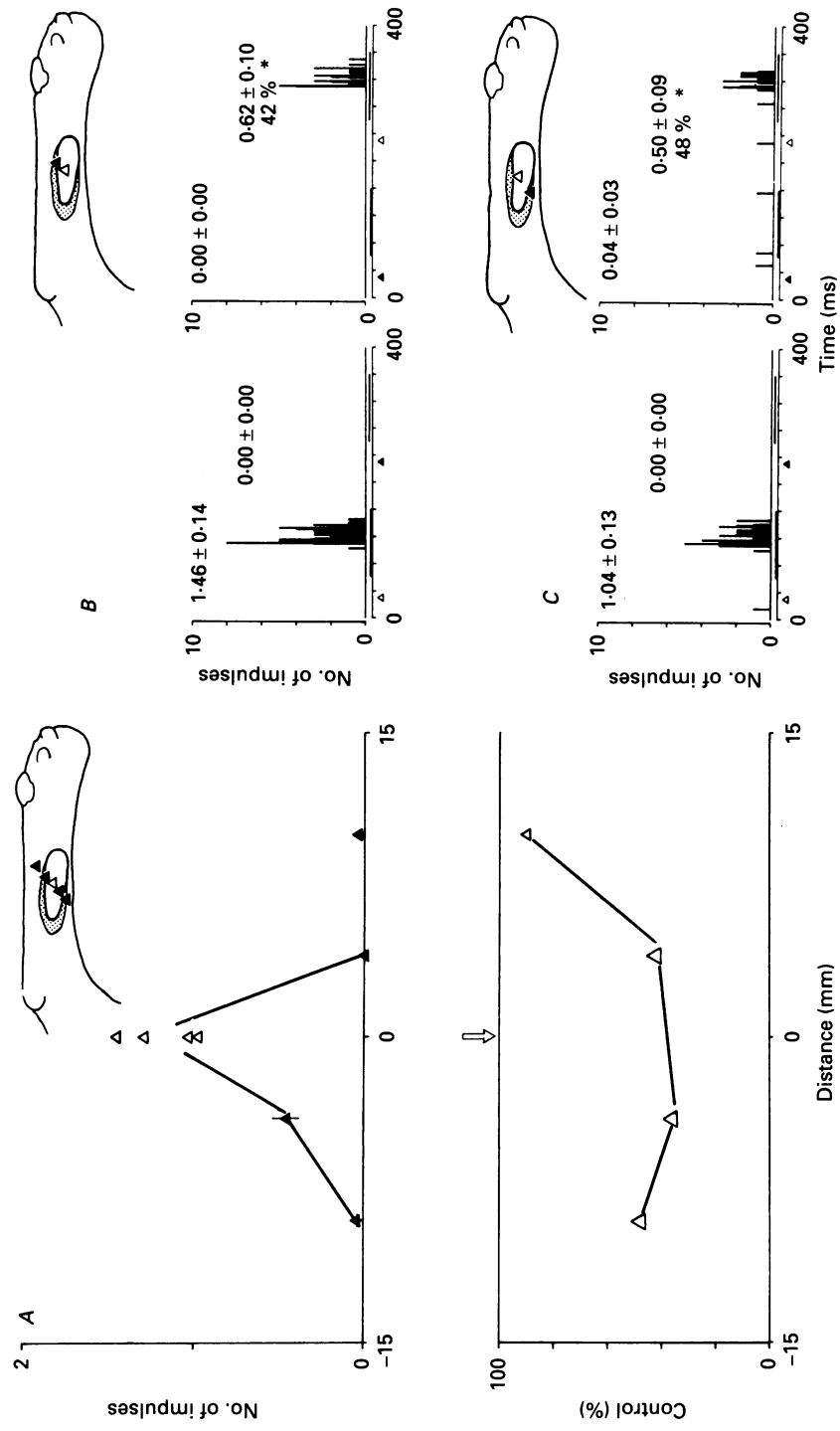

Fig. 5. *A*, summary diagram, similar to previous figures, of the responses of a hair-only SCT unit. Excitation was elicited from the fixed point and only one of the other points tested. Significant inhibition of the response at the fixed point was elicited by conditioning at two points outside the excitatory receptive field. The unshaded outline of the excitatory receptive field is shown, and the stippling shows the area where afferent inhibition but no excitation could be elicited. *B* and *C*, peristimulus time histograms for the two points in *A* where afferent inhibition but no excitation could be elicited. Binwidth 1 ms, 50 sweeps.

therefore partly inhibition of the background and partly of the response, and the two are not distinguishable. For this reason we use the inhibition of the response to the fixed stimulus by the variable position stimulus as the best indication of the spatial spread of in-field afferent inhibition.

Where a unit had an excitatory receptive field at the larger end of the range studied, the spatial spread of in-field afferent inhibition was less, and sometimes much less, than the excitatory field. An example is shown in Fig. 4, where the excitatory receptive field is about 140 mm across and the spatial spread of inhibition is about 60 mm.

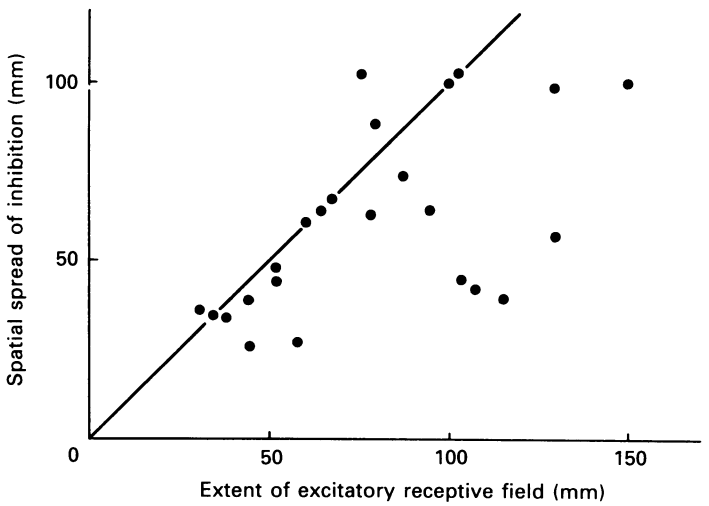

Fig. 6. Spatial spread of inhibition of fixed point plotted against maximum extent of excitatory receptive field for twenty-three SCT units. The spatial spread of inhibition is limited to about 100 mm or less.

Afferent inhibition from outside the excitatory receptive field

In two units stimulus points were found, just outside the excitatory receptive field, from which no impulses were elicited, but which produced significant inhibition of a subsequent response from a point inside the excitatory receptive field at an interval of 200 ms. Figure 5 shows the receptive field profile of one of these units and also two pairs of histograms which demonstrate the inhibition without previous impulse responses. This particular unit was extensively tested, and the inhibition was produced repeatedly from several different points just outside the excitatory receptive field. Other units were tested for inhibition produced from outside the excitatory receptive field, but it was not found, even when one stimulus was just outside the field and the other nearby and just within.

Figure 6 summarizes the maximum extents of the excitatory receptive fields and the spatial spread of in-field afferent inhibition for the twenty-three units studied. The spatial spread of inhibition is generally within the excitatory receptive field, except in two units where it spread slightly outside. In six units, the spatial spread of inhibition was co-extensive with the excitatory receptive field; in the remaining

fifteen units, the spatial spread of inhibition was limited to a part of the excitatory receptive field, and did not exceed about 100 mm in extent.

No examples of an asymmetrical spread of in-field afferent inhibition were found when the fixed stimulus was at or near the centre of the receptive field; in this sample there is no evidence for a directional organization.

DISCUSSION

The interstimulus intervals used in the present study (100–300 ms) ensure that the observed in-field afferent inhibition of transmission is not due to activation of the inhibitory receptive fields which produce IPSPs in SCT cells and which may or may not overlap the excitatory receptive field, since this inhibition is over by about 60 ms (Hongo *et al.* 1968; Brown *et al.*, 1987*c*). We are therefore confident that we are studying the in-field afferent inhibition which follows excitation, does not involve IPSPs in SCT cells and lasts 700 ms or more (Brown *et al.* 1987*b*, *c*). Our results show several features of this in-field afferent inhibition.

First, there clearly is spatial spread of the inhibition, in that a stimulus to a point in the excitatory receptive field will inhibit responses elicited from other points, as well as from the point itself. Second, the inhibition can, in a minority of units, be produced by a stimulus just outside the excitatory receptive field; although in most units it could not, even when one stimulus was just inside the field and the other nearby and just outside. Third, there are no clear asymmetrical or directional features to the inhibition. Fourth, and most intriguing, is the finding, especially evident in the larger receptive fields, that the spread of the in-field afferent inhibition is restricted to subdomains no more than 100 mm across within the excitatory receptive field.

Most of these features are in marked contrast to the shorter-lasting inhibition associated with IPSPs in the SCT cells. In the latter case, IPSPs can be evoked from areas both inside and outside the excitatory receptive fields. These inhibitory fields overlap the excitatory fields to varying degrees; and in some units they are widely separated from the excitatory fields (Hongo *et al.* 1968; Brown *et al.* 1987*c*). This latter arrangement might give a basis for directional sensitivity, since a stimulus moving across the skin will give a different response in an SCT cell depending on whether it meets an excitatory or an inhibitory zone first; however, direct evidence for directional sensitivity is not available. The afferent inhibition which we have found in two units from outside the excitatory receptive field is restricted to a narrow strip, probably corresponding to a subliminal fringe of excitation, such as is illustrated in Fig. 6 of Brown *et al.* (1987*c*).

There are some contrasts with the properties of cuneothalamic cells found by Jänig *et al.* (1977) in barbiturate-anaesthetized cats. Afferent inhibition was of much shorter duration (up to about 250 ms) in cuneothalamic cells, and the spatial spread was generally greater than the excitatory receptive field, giving an inhibitory surround. Afferent inhibition was more effective between points close together in the receptive field than between more widely spaced points, suggesting that there may be a substructure in the organization of afferent inhibitory input to the cuneothalamic cells; however, localized subdomains were not noted by Jänig *et al.*

(1977). The present results, and those in the accompanying paper on the lateral cervical nucleus (Brown, Maxwell & Short, 1989) emphasize that the in-field afferent inhibition known to exist in the cuneothalamic–cortical system (Jänig *et al.* 1977, 1979; Laskin & Spencer 1979), occurs also in the spinocervical–thalamic–cortical system and is already present at the level of the spinal cord.

The hair follicle excitatory input to SCT cells has both monosynaptic and polysynaptic components (Brown *et al.* 1987*c*); the present methods do not distinguish between the two. However, Brown *et al.* (1987*c*) showed that monosynaptic excitatory postsynaptic potentials (EPSPs) are mainly unaffected by the in-field afferent inhibition of transmission, which acts principally on the polysynaptic components. Brown *et al.* (1987*c*) also could find no evidence for recurrent inhibition in SCT cells: transmission was suppressed even when the conditioning stimulus evoked only EPSPs and not action potentials; furthermore, direct intracellular excitation of the SCT cell did not suppress subsequent transmission from hair-follicle afferent fibres. In a previous intracellular study, Hongo *et al.* (1968) also found no evidence for recurrent inhibition in SCT cells. The present results provide further indirect evidence for the same conclusion; inhibition restricted to part of the excitatory receptive field could not be produced by recurrent inhibition or by post-activation depression of the SCT cell; also, we confirm the occasional occurrence of a subliminal fringe which produces inhibition without itself evoking impulses in the SCT cell.

The background discharge was also suppressed by stimulation of hair-follicle afferents in the present study. If, as suggested by the work of Brown *et al.* (1987*c*), it is transmission through the excitatory interneurones which is suppressed, then this inhibition of the background discharge implies that the latter is generated by activity in these interneurones. A reduced background discharge may enhance the acuity of the system in detecting a stimulus.

The inhibitory subdomains therefore probably correspond to an organization of the input to a SCT cell presynaptic to the cell itself. Since the effect is almost entirely on the polysynaptic input, it may indicate that this arises from several interneurones with smaller excitatory fields than the SCT cell, and that the observed afferent inhibition arises from inhibition of one of these interneurones by a stimulus within its excitatory field. Alternatively, it may be that there are inhibitory interneurones with input from subdomains, and these act either on the excitatory interneurones directly or on the axon terminals of the afferent fibres. These alternatives can only be resolved when the interneurones have been identified and studied. The functional significance of suppressed transmission restricted to subdomains within the excitatory field remains a matter for speculation. Nevertheless, there are several possible consequences of the organization which merit discussion.

Spinocervical tract cells exhibit a gradient of sensitivity to stimulation within their excitatory receptive fields; the response magnitudes decline as the stimulus is moved sequentially from the centre to the periphery of the field (Brown, Noble & Rowe, 1986). The receptive field response profiles of these cells have been obtained, however, using punctate stimuli to small groups of hairs at discrete locations on a grid within the receptive field. Given the in-field afferent inhibition following excitation through hair follicle afferent fibres, we should expect the response profiles

to a moving stimulus to be different from those obtained using punctate stimuli. A stimulus moving into and across a receptive field might be expected to evoke a different response profile, owing to the subsequent inhibition generated as the stimulus moves across the receptive field. The weak responses evoked from the periphery of the field may be totally suppressed. A stimulus within the excitatory receptive field would therefore reduce the effective spatial extent of the excitatory receptive field; this would also reduce the number of SCT cells activated by a subsequent stimulus and might thus increase the spatial acuity of the SCT system.

The excitatory input from hair follicle afferent fibres is very potent: even a single action potential in a sensory afferent fibre may evoke several impulses in a SCT cell (Brown *et al.* 1987*a*). A large proportion of the cells receive input from the toes (Brown, Fyffe, Noble, Rose & Snow, 1980) and in the absence of inhibition there would be a large barrage of input in the SCT when the animal is walking or running about. The suppression following activation of the SCT may act to reduce its activity in the mobile cat.

This work was supported by an MRC programme grant to Professor A. G. Brown. We thank Professor Brown and Dr D. J. Maxwell for collaborating in an experiment and for regular discussion and comment. Animals were held in the Wellcome Animal Research Unit, Faculty of Veterinary Medicine, University of Edinburgh.

REFERENCES

BROWN, A. G., FYFFE, R. E. W., NOBLE, R., ROSE, P. K. & SNOW, P. J. (1980). The density, distribution and topographical organization of spinocervical tract neurones in the cat. *Journal of Physiology* **300**, 409–428.

BROWN, A. G., KOERBER, H. R. & NOBLE, R. (1987*a*). Excitatory actions of single impulses in single hair follicle afferent fibres on spinocervical tract neurones in the cat. *Journal of Physiology* **382**, 291–312.

BROWN, A. G., KOERBER, H. R. & NOBLE, R. (1987*b*). Actions of trains and pairs of impulses from single primary afferent fibres on single spinocervical tract cells in cat. *Journal of Physiology* **382**, 313–329.

BROWN, A G., KOERBER, H. R. & NOBLE, R. (1987*c*). An intracellular study of spinocervical tract cell responses to natural stimuli and single hair afferent fibres in cats. *Journal of Physiology* **382**, 331–354.

BROWN, A. G., MAXWELL, D. J. & SHORT, A. D. (1989). Receptive fields and in-field afferent inhibition of neurones in the cat's lateral cervical nucleus. *Journal of Physiology* **413**, 119–137.

BROWN, A. G., NOBLE, R. & ROWE, M. J. (1986). Receptive field profiles and integrative properties of spinocervical tract cells in the cat. *Journal of Physiology* **374**, 335–348.

GARDENER, E. P. & COSTANZO, R. M. (1980). Spatial integration of multiple-point stimuli in primary somatosensory cortical receptive fields of alert monkeys. *Journal of Neurophysiology* **43**, 420–443.

HONGO, T., JANKOWSKA, E. & LUNDBERG, A. (1968). Post-synaptic excitation and inhibition from primary afferents in the spinocervical tract. *Journal of Physiology* **199**, 569–592.

JÄNIG, W., SCHOULTZ, T. & SPENCER, W. A. (1977). Temporal and spatial parameters of excitation and afferent inhibition in cuneothalamic relay neurons. *Journal of Neurophysiology* **40**, 822–835.

JÄNIG, W., SPENCER, W. A. & YOUNKIN, S. G. (1979). Spatial and temporal features of afferent inhibition of thalamocortical relay cells. *Journal of Neurophysiology* **42**, 1450–1460.

LASKIN, S. E. & SPENCER, W. A. (1979). Cutaneous masking. II. Geometry of excitatory and inhibitory receptive fields of single units in somatosensory cortex of the cat. *Journal of Neurophysiology* **42**, 1061–1082.

NOBLE, R. & SHORT, A. D. (1988). Spatial spread of late inhibitory input to spinocervical tract cells in the chloralose-anaesthetized cat. *Journal of Physiology* **398**, 30*P*.